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Climate change and the outbreak ranges of two North American bark beetles

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Abstract

1 One expected effect of global climate change on insect populations is a shift in geographical distributions toward higher latitudes and higher elevations. Southern pine beetle *Dendroctonus frontalis* and mountain pine beetle *Dendroctonus ponderosae* undergo regional outbreaks that result in large-scale disturbances to pine forests in the south-eastern and western United States, respectively.

2 Our objective was to investigate potential range shifts under climate change of outbreak areas for both bark beetle species and the areas of occurrence of the forest types susceptible to them.

3 To project range changes, we used discriminant function models that incorporated climatic variables. Models to project bark beetle ranges employed changed forest distributions as well as changes in climatic variables.

4 Projected outbreak areas for southern pine beetle increased with higher temperatures and generally shifted northward, as did the distributions of the southern pine forests.

5 Projected outbreak areas for mountain pine beetle decreased with increasing temperature and shifted toward higher elevation. That trend was mirrored in the projected distributions of pine forests in the region of the western U.S. encompassed by the study.

6 Projected outbreak areas for the two bark beetle species and the area of occurrence of western pine forests increased with more precipitation and decreased with less precipitation, whereas the area of occurrence of southern pine forests decreased slightly with increasing precipitation.

7 Predicted shifts of outbreak ranges for both bark beetle species followed general expectations for the effects of global climate change and reflected the underlying long-term distributional shifts of their host forests.

Keywords Climate change, *Dendroctonus frontalis*, *Dendroctonus ponderosae*, discriminant analysis, geographical range shift, insect outbreak.

Introduction

General circulation models (GCMs) of global climate predict temperature increases from 1 °C to over 5 °C in central North America under doubled CO_2 levels (Giorgi *et al.*, 1998). Such increases could produce profound changes in the forests of the continent (Shriner & Street, 1998). The geographical ranges of many tree species are predicted to shift northward (Davis & Zabinski, 1992; Dyer, 1995; Iverson *et al.*, 1999), and the extent to which they do so is likely to alter stand composition across forested landscapes. Insect herbivores of tree species will also shift ranges to follow their hosts (Williams & Liebhold, 1997), and altered trophic interactions under changed climate may further confound predictions of distributions over long periods of time (Franklin *et al.*, 1992; Davis *et al.*, 1998; Harrington *et al.*, 1999).

The tree-killing bark beetle (Coleoptera: Scolytidae) species, southern pine beetle *Dendroctonus frontalis*

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Zimmerman and mountain pine beetle *Dendroctonus ponderosae* Hopkins, both undergo outbreaks and cause widespread disturbances in pine forests of North America (Price *et al.*, 1998; Raffa, 1988). The range of southern pine beetle includes the south-eastern United States, Mexico and Central America and extends as far north as New Jersey and as far south as Honduras (Payne, 1980). The range of mountain pine beetle encompasses a large region of western North America, extending into South Dakota to the east, south-western Canada to the north, and New Mexico and Arizona to the south (Amman *et al.*, 1985). Mountain pine beetle also inhabits a wide range in elevation, from sea level in British Columbia to over 3300 m in southern California (Amman *et al.*, 1985). Although the causes of outbreaks of tree-killing bark beetles are far from clear, they often begin where large numbers of trees are stressed or damaged, and outbreaks are sustained by the availability of stands of mature trees (Flamm *et al.*, 1988; Raffa, 1988). Both species have preferred host species, but during outbreaks they attack most pine species in their ranges (Payne, 1980; Amman *et al.*, 1985). Because most *Dendroctonus* species must kill their hosts in order to reproduce (Flamm *et al.*, 1988; Raffa, 1988), outbreaks can result in widespread stand mortality, which may hasten regeneration or the conversion to other forest types (Amman *et al.*, 1985).

Climate change may affect the dynamics of herbivorous insect populations in two ways: directly, through the physiological processes of individual insects, and indirectly, through their host plants and natural enemies (Mattson & Haack, 1987; Heliövaara *et al.*, 1991; Porter *et al.*, 1991; Cammell & Knight, 1992; Landsberg & Stafford Smith, 1992). Both bark beetle species are likely to be affected directly and indirectly by climate change as a result of specific life history characteristics. Both can produce variable numbers of generations per year in different parts of their geographical ranges, dependent upon climatic conditions (although it must be noted that mountain pine beetle is univoltine or less in our study region) (Payne, 1980; Raffa, 1988). Both overwinter in various immature stages in the phloem tissue of their hosts (Thatcher & Barry, 1982; Raffa, 1988). Survival during hibernation is probably closely related to winter temperatures, with death occurring rapidly below critical thresholds (Bentz & Mullins, 1999; Ungerer *et al.*, 1999; Lombardero *et al.*, 2000). On the other hand, neither species undergoes diapause (Payne, 1980; Bentz & Mullins, 1999), and thus, development can proceed over winter as temperature permits.

Indirect effects of climate change may occur through interactions with symbionts and hosts. Adults of both species transport phytopathogenic fungi into the host tree that hasten tree killing and facilitate beetle colonization (Bridges, 1985; Flamm *et al.*, 1988; Raffa, 1988). Survival and growth of those fungi may be affected, albeit unpredictably, by changes in climate (Heliövaara *et al.*, 1991). Water stress on host trees induced by regional drought has been proposed as a cause of bark beetle outbreaks in several investigations (King, 1972; Kalkstein, 1976; Shrimpton, 1978; Gagne *et al.*, 1980). Clearly, changes in climate, particularly toward hotter and drier conditions, may increase the frequency of outbreaks if this mechanism is valid. However, Reeve *et al.* (1995) offer another hypothesis based on a conceptual model of the effects of water availability on carbon budgets of pine. They suggest that 'drought may increase or decrease suitability for bark beetles depending on the initial water status of the trees and the severity of the drought' and that a surfeit of water may also render pines more suitable for bark beetles.

As a result of many of these direct and indirect factors, climate change may also simply allow bark beetles to move northward or higher in elevation into other ranges of their host species or the ranges of new potential hosts. We address this possibility here. In the following, we develop canonical discriminant function models of the occurrence of host forests and bark beetle outbreaks under ambient climatic conditions. We then use the models to predict potential range shifts of forest and insect populations over wide geographical regions in the United States under several scenarios of change in temperature and precipitation.

Methods

Map development

Maps of bark beetle outbreaks, climatic variables and susceptible forest types were developed using the Idrisi geographical information system (Eastman, 1989). Idrisi is a raster-based GIS in which objects are represented in space by a matrix of 'rasters', which are square grid cells. Details of the production and processing of maps are provided in Williams & Liebhold (1997).

Annual maps of counties in the south-eastern United States undergoing outbreaks of southern pine beetle over the period 1960–1994 were compiled from records collected by the United States Department of Agriculture (USDA) Forest Service and state agencies (Price *et al.*, 1998). Vector coverages of county maps were converted to maps of 5 km × 5 km rasters for analysis. A county was considered to be in outbreak status if it averaged more than one infestation 'spot' per 1000 acres of susceptible host forest (i.e. loblolly shortleaf pine and oak-pine forest type groups). A spot is a cluster of infested trees (Coulson, 1980). The minimum size of a spot is typically 5–10 trees in state monitoring programmes (Price *et al.*, 1998). The annual maps were superimposed, and county areas were added up year-by-year to produce a map of the total area of outbreaks that was a basis for analyses. The total area of south-eastern counties in outbreak status for at least one year was 837 075 km^2.

Unlike the county maps for southern pine beetle, annual maps of mountain pine beetle depicted actual areas infested as detected in aerial surveys. Maps for the states of Idaho, Montana and Wyoming (north-western corner only) during 1980–1995 were digitized and assembled from paper maps provided by state and federal agencies (e.g. Beckman *et al.*, 1996; McConnell, 1996). Annual maps of infested areas in the states of Washington and Oregon were obtained from Forest Pest Management in the USDA Forest Service Pacific North-west Region as vector polygon coverages. The vector coverages were converted to maps of 2 km × 2 km rasters before merging with maps for the other three states. All maps were developed from historical aerial sketch maps of bark beetle damage. A map of the total area of mountain pine beetle outbreaks was developed by overlaying maps from all years. The total area of grid cells in the five-state area with outbreaks during at least one year was 79 400 km^2.

It should be noted as a caveat that the outbreak areas used in the following analyses did not cover the entire ranges of either bark beetle species. Southern pine beetle occurs in the south-western United States, Mexico and Central America in addition to the south-eastern U.S. (Flamm *et al.*, 1988). The range of mountain pine beetle extends as far south as the states of Arizona and New Mexico and as far north as the southern half of the Canadian province of British Columbia (Amman *et al.*, 1985), as well as including the five western states already mentioned.

Maps of historical climatic variables in the conterminous United States were obtained from the Global Ecosystems Database (National Oceanographic and Atmospheric Administration, 1993). The gridded maps of monthly means of daily air temperatures were interpolated from weather station data averaged over the 40-year period from 1948 to 1987. The interpolation, which accounted for the effect of elevation on temperature, involved several steps. First, station air temperatures were converted to their equivalents at sea level using station elevations and the hydrostatic equation. Second, the corrected station temperatures were interpolated to a 10 km × 10 km grid using a simple linear inverse distance squared algorithm (Isaaks & Srivastava, 1989). Finally, the interpolated temperature maps were used along with a 10 km × 10 km digital elevation model map to create a map of gridded temperature estimates corrected for the effects of elevation. Maps of historical total monthly precipitation over the same grid were developed using the PRISM model (Daly *et al.*, 1994).

Maps of forest types susceptible to the bark beetle species were developed from a map of forest type groups in the conterminous U.S. produced by the USDA Forest Service from advanced very high resolution radiometer (AVHRR) satellite imagery (Zhu & Evans, 1992). For use in the mountain pine beetle analyses, we extracted the distributions of the lodgepole pine, ponderosa pine, and western white pine forest type groups, which contain the primary host species of this bark beetle (Raffa, 1988) (Fig. 1a). Similarly, we used the distributions of the loblolly shortleaf pine and oak-pine forest type groups as forests susceptible to southern pine beetle outbreaks in the analyses (Pye, 1993) (Fig. 1c). It must be noted that the areas classified simply as 'non-forest' (and hence, not susceptible to bark beetle outbreaks) were treated differently between the regions. Non-forest lands were excluded from the analyses of south-eastern forests because they contained high proportions of land under human use, including agricultural, urban and suburban areas. Because non-forest areas were not classified further as to land use, inclusion of those areas would have produced classification errors in the discriminant analysis of south-eastern forests. On the other hand, non-forest land was included in the analysis of western forests because the north-western region of the U.S. contains large areas that are naturally unforested, such as grasslands. In addition, the forest type group map was developed from AVHRR images obtained in 1991. The use of a single land cover 'snapshot' in time may have introduced errors when applied to bark beetle infestation maps extending over as many as 35 years, especially in the south-eastern U.S., where agricultural land use patterns have shifted over the period from 1960 to 1994 (Anon, 1989).

The original maps came at a variety of resolutions (Table 1). As a compromise between the extremes of the map resolutions in the western states, maps were set at the resolution of the mountain pine beetle infestation maps for analyses. Redundancy of the values of climatic variables, which were mapped with much larger cells originally, may have reduced the goodness-of-fit of the mountain pine beetle analyses. In contrast, maps of southern pine beetle infestations were summarized by county. For those analyses, climatic variables and the presence of susceptible forest type were averaged in individual counties. The analysis of south-eastern forests was carried out on observations in 5 km × 5 km cells.

Predicting potential changes in the geographical distribution of bark beetle outbreaks and pine forests involved two steps: (1) fitting their distributions as functions of the environmental variables and (2) extrapolating new distributions using the fitted functions under climate change scenarios. Because we were interested only in predicting qualitative outbreak patterns, we simplified the frequency maps by reclassifying each into two categories of cells: those that were never infested and those that were infested in at least one year (Figs 2a and c).

Statistical analysis

We used a canonical discriminant function as our model for predicting the occurrences of bark beetle outbreaks and susceptible forest types. A canonical discriminant function predicts values of a canonical variable that has two or more discrete states as a linear function of a number of independent variables (Manly, 1986)

$$D = a_1X_1 + a_2X_2 + \cdots + a_nX_n$$

In our case, the canonical variable, D, for an individual cell was classified as infested (1) or not infested (0) and its value depended on the values of the climatic and forest variables (X_n). Similarly, for modelling forest distributions, the canonical variable had two discrete states, presence (1) or absence (0) of susceptible pine forest types, which depended upon the climatic variables.

Rather than fitting the two functions with all 24 or 25 independent variables (i.e. 12 monthly mean daily temperatures, 12 monthly precipitation means, and occurrence of susceptible forest types), we included only those that were significant in explaining the occurrence of bark beetle outbreaks or pine

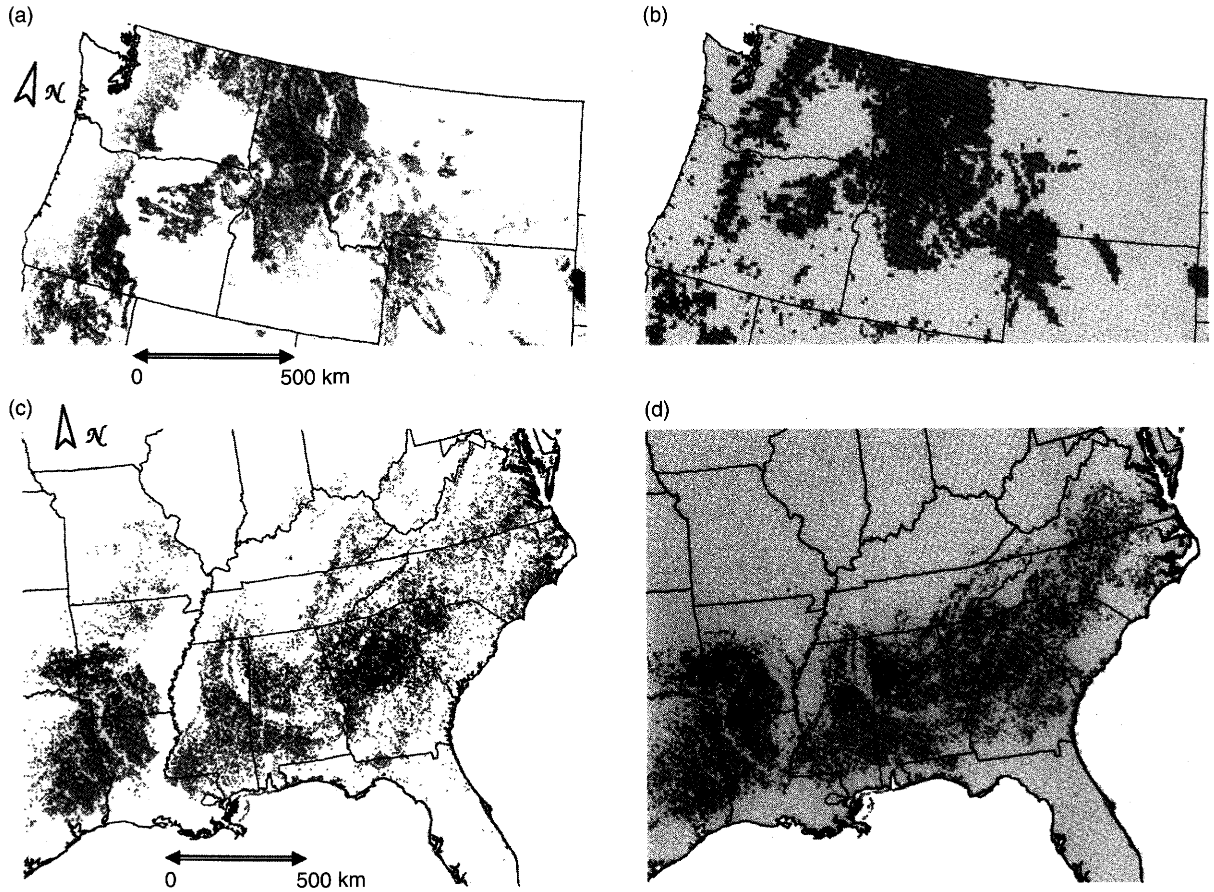

Figure 1 Pine forest type groups susceptible to the bark beetle species and areas predicted to be occupied by susceptible forests under ambient climatic conditions. Light shading (b, d) indicates the remainders of the predicted regions used in the analyses. (a) Ponderosa pine, lodgepole pine, and western white pine, susceptible to mountain pine beetle, (b) pine forest areas predicted to be susceptible to mountain pine beetle, (c) loblolly shortleaf pine and oak-pine, susceptible to southern pine beetle, (d) pine forest areas predicted to be susceptible to southern pine beetle.

forests. We used a stepwise procedure that evaluated variables individually for their contributions to the goodness-of-fit of the discriminant function (SAS Institute, 1990).

We used only climatic variables as independent variables in the analyses because of their obvious correlation with climate change. Site variables, such as soil type, drainage class, aspect and elevation, also may affect the presence of a pine forest type and bark beetle outbreak in an area. However, we chose not to include them in the analyses because of their static nature. Nevertheless, such factors are important in practice because there are some sites in which trees cannot grow. Clearly, site variables may become important in limiting establishment as forests move into new areas under the influence of climate change.

Table 1 Original resolutions of mapped variables

Variable	Resolution
Temperature and precipitation	10 km × 10 km cells
Forest type groups	1 km × 1 km cells
Mountain pine beetle infestation	2 km × 2 km cells
Southern pine beetle outbreak	County

Climate change scenarios

Given the fitted canonical discriminant functions for the occurrence of pine forests, we modified the equation to extrapolate climate change effects as follows:

$$CVF = a_1(T_1 + \Delta T_1) + \cdots + b_{12}(P_{12} + \Delta P_{12})$$

where CVF is the canonical variable for forest type, T_i is the mean temperature in month i, ΔT_i is the temperature change for a climate change scenario, P_i is mean precipitation in month i, and ΔP_i is the precipitation change. Similarly, we modified the discriminant equation for the occurrence of bark beetle outbreaks as

$$CVB = a_1(T_1 + \Delta T_1) + \cdots + b_{12}(P_{12} + \Delta P_{12}) + cF$$

where F is the occurrence of a susceptible forest type (for mountain pine beetle) or its proportion of occurrence in a

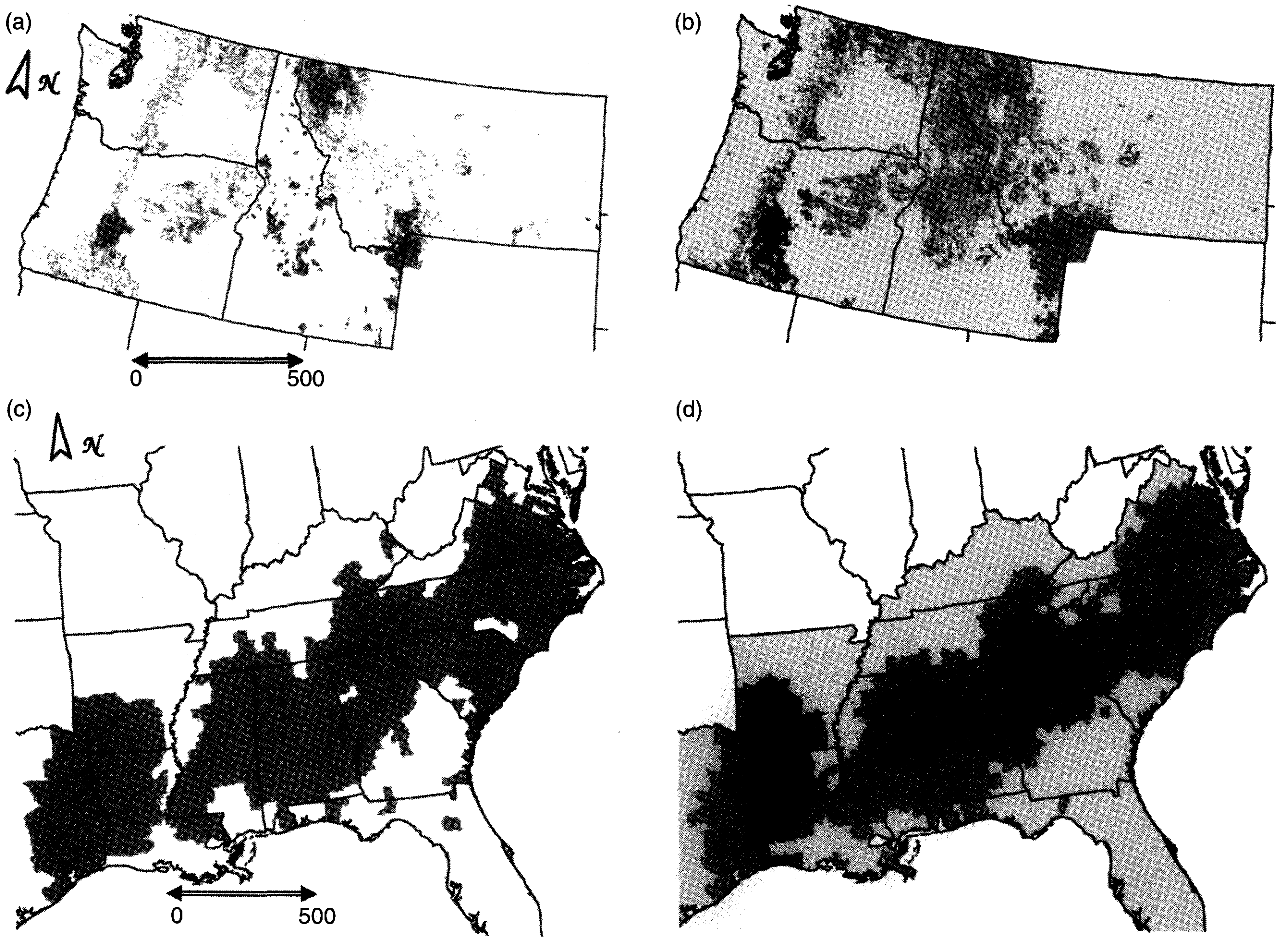

Figure 2 Outbreak areas of bark beetle species and areas predicted to have bark beetle outbreaks under ambient climatic conditions and observed forest distributions. Light shading (b, d) indicates the remainders of the predicted regions used in the analyses. (a) Mountain pine beetle in the north-western U.S. during 1980–1995, (b) predicted mountain pine beetle outbreaks, (c) southern pine beetle in counties of the south-eastern U.S. during 1960–1994, (d) predicted southern pine beetle outbreaks.

county (for southern pine beetle). Using the relationship, we reclassified each grid cell by inserting ambient values and change values for the environmental variables. Developing the outbreak scenarios was a two step process. First, we used the forest discriminant functions to predict future pine forest distributions. Second, we used those forest scenarios along with the respective changes in climatic variables in the outbreak discriminant functions to predict future bark beetle outbreak areas.

We used simple incremental changes in temperature (i.e. $+2, +4$ and $+8\,^{\circ}\mathrm{C}$) and precipitation ($\pm 0.5\,\mathrm{mm/day}$) as our climate change scenarios. We acknowledge that changing climatic variables uniformly across large geographical regions and over the seasons of the year may be unrealistic from a 'real world' standpoint, but doing so provides the simplest and most consistent test of our models. Attempts to use predictions of general circulation models (GCMs) proved unsatisfactory because of their large spatial scales (Cooter *et al.*, 1993), which led to regional discontinuities in our predictions of forest type occurrence and bark beetle outbreak areas.

Results

Discriminant analyses

The four discriminant functions fitted to the incidence of pine forest types and bark beetle outbreaks were all highly significant, as indicated by Wilk's lamba, and included most of the available environmental variables (Table 2). However, individual grid cells on a map and county areas do not represent independent observations, and the high level of statistical significance was undoubtedly affected by the spatial autocorrelation inherent in the map data (Gumpertz *et al.*, 2000). Squared canonical correlations, which are similar to R^2 values for linear regressions, were relatively low for three of the relationships. However, the squared canonical correlation for southern pine beetle exceeded 0.5, indicating a relatively good fit for that discriminant function. The error rates, as indicated by the proportions of cells misclassified, inversely reflected the relative goodness-of-fit of the relationships. Accordingly, the function for southern pine beetle outbreaks had proportions

Table 2 Characteristics of canonical discriminant functions for the occurrence of pine forest type groups and bark beetle outbreaks. The *F*-values for all Wilks's lambdas were highly significant

Dependent variable	Sample size	Number of independent variables	Squared canonical correlation	Wilks's lambda	Proportion of cells misclassified: False positive	Proportion of cells misclassified: False negative
Western pine forests	328114	22	0.228	0.772	0.204	0.280
Mountain pine beetle	254974	24	0.151	0.849	0.191	0.282
Southern pine forests	41731	20	0.294	0.706	0.287	0.210
Southern pine beetle	1065	15	0.527	0.472	0.142	0.142

of misclassifications of 0.14, whereas that for susceptible southern pine forests had proportions in the range 0.21–0.29. It is notable that false positive misclassifications (i.e. cases in which the discriminant function predicted presence where none was observed) were more prevalent in analyses in the south-eastern region, whereas false negative misclassifications (i.e. predictions of absence where forests or outbreaks were observed) were more prevalent in the western region.

Goodness-of-fit of the relationships for susceptible pine forest occurrence and bark beetle outbreaks may be assessed visually by comparing the actual distributions (Figs 1a and c, 2a and c, respectively) with those predicted under ambient environmental conditions (Figs 1b and d, 2b and d, respectively). (Note that the predictions of bark beetle outbreak areas in Figs 2b and d used the observed forest type distributions.) The areas predicted to be occupied by western pine forests (Fig. 1b) and south-eastern pine forests (Fig. 1d) were similar in geographical location to those observed (Figs 1a and c, respectively). However, the predicted areas generally were more continuous. The generally large grid cells of the predicted forest distributions resulted from the coarse resolution of the climatic maps (i.e. 10 km) relative to the finer resolutions used for the analyses (i.e. 2 km for western forests and 5 km for south-eastern forests). The predicted distribution for mountain pine beetle outbreaks (Fig. 2b) was similar geographically to the observed distribution (Fig. 2a), but clearly was larger than that observed. In contrast, the predicted distribution of southern pine beetle (Fig. 2d) provided a relatively good fit to the observed distribution (Fig. 2c).

Six of the first seven variables to be selected by the stepwise process for the discriminant function for western pine forests were monthly temperatures, although mean temperature in June clearly was most strongly correlated with the forest distribution (Table 3). The mountain pine beetle outbreak distribution was most strongly correlated with susceptible forest type, with climatic variables contributing relatively less to the relationship. Two precipitation variables, for the months of February and August, were most strongly correlated with the south-eastern pine forest distribution (Table 4). Occurrence of the susceptible forest type was selected first for the southern pine beetle relationship and was followed by seven monthly precipitation variables.

Climate change scenarios

Area changes projected for western pine forests (Table 5) and for infestations by mountain pine beetle (Table 6) were very similar. Areas decreased as temperature increased. Areas projected at an increase of 8 °C approached just 21–22% of those under ambient temperature without changes in precipitation. Susceptible pine forest and outbreak ranges increased in area with incremental increases of 0.5 mm/day in precipitation. These patterns were evident in maps of projected mountain pine beetle outbreak areas under four temperature and two precipitation change scenarios (Fig. 3). The loss of area at higher temperatures reflected

Table 3 First ten variables selected stepwise for the canonical discriminant functions relating presence of western pine forest type groups and mountain pine beetle outbreaks to environmental factors

Step	Western Pine forests: Variable	Western Pine forests: Partial R^2	Mountain pine beetle: Variable	Mountain pine beetle: Partial R^2
1	June temperature	0.120	Forest type	0.086
2	Aug. temperature	0.006	Apr. temperature	0.017
3	June precipitation	0.005	May precipitation	0.005
4	Mar. temperature	0.005	July precipitation	0.007
5	Nov. temperature	0.029	Mar. temperature	0.007
6	Feb. temperature	0.014	May temperature	0.010
7	Sep. temperature	0.009	June temperature	0.008
8	Sep. precipitation	0.010	Mar. precipitation	0.001
9	Jan. precipitation	0.011	Feb. precipitation	0.002
10	Oct. precipitation	0.017	June precipitation	0.002

Table 4 First ten variables selected stepwise for the canonical discriminant functions relating presence of southern pine forest type groups and southern pine beetle outbreaks to environmental factors

	Southern Pine forests		Southern pine beetle	
Step	Variable	Partial R^2	Variable	Partial R^2
1	Feb. precipitation	0.096	Forest type	0.293
2	Aug. precipitation	0.074	Oct. precipitation	0.038
3	Jan. temperature	0.059	Jan. precipitation	0.038
4	Dec. temperature	0.045	May precipitation	0.094
5	Nov. temperature	0.020	June precipitation	0.025
6	Oct. precipitation	0.005	Mar. precipitation	0.006
7	Mar. temperature	0.003	July precipitation	0.006
8	Aug. temperature	0.011	Sep. precipitation	0.005
9	Feb. temperature	0.007	July temperature	0.006
10	May precipitation	0.004	June temperature	0.025

Table 5 Projected actual areas in km^2 and relative areas (in parenthesis, % of area projected at ambient conditions) occupied by susceptible pine forest type groups in the western United States under climate change scenarios (total land surface area = 1 320 832 km^2)

	Precipitation change		
Temperature change	−0.5 mm/day	Ambient	+0.5 mm/day
Ambient	329 508 (84)	393 296 (100)	460 680 (117)
+2 °C	235 808 (60)	280 036 (71)	326 372 (83)
+4 °C	160 392 (41)	192 220 (49)	232 868 (59)
+8 °C	63 408 (16)	81 792 (21)	102 432 (26)

the smaller land areas available at higher elevations. The gradual thinning out of outbreak distributions along their margins as temperature increased suggested the effects of an elevational gradient. To examine this effect, we superimposed each individual temperature change scenario map on a map of elevation and computed the average elevation encompassed in the area of that scenario. The average elevations of the outbreak areas at ambient temperature, + 2, + 4 and + 8 °C were 1684, 1764, 1829 and 1926 m, respectively. Averaged over all temperature change scenarios, the mountain pine beetle outbreak areas increased in elevation by 30.2 m with each 1 °C increase. A similar analysis for the western pine forests yielded an average increase in elevation of 15.5 m per 1 °C increase.

Area changes projected for susceptible south-eastern pine forests (Table 7) and southern pine beetle outbreaks (Table 8) exhibited different trends. Areas for both increased with increases in temperature. Under the + 8 °C scenario, pine forests were projected to increase in area by almost 190% of projections under ambient temperature and precipitation, whereas southern pine beetle outbreak areas were projected to increase by 156% of those under ambient conditions. Similar to the situation in the western U.S., the area occupied by southern pine beetle outbreaks was projected to increase with incremental increases in precipitation.

Table 6 Projected actual areas in km^2 and relative areas (in parenthesis, % of area projected at ambient conditions) infested by mountain pine beetle in the western United States under climate change scenarios (total land surface area = 1 320 832 km^2)

	Precipitation change		
Temperature change	−0.5 mm/day	Ambient	+0.5 mm/day
Ambient	332 192 (82)	403 660 (100)	478 808 (119)
+2 °C	237 624 (59)	291 008 (72)	347 468 (86)
+4 °C	159 900 (40)	203 012 (50)	253 856 (63)
+8 °C	62 888 (16)	87 656 (22)	117 012 (29)

Table 7 Projected actual areas in km^2 and relative areas (in parenthesis, % of area projected at ambient conditions) occupied by susceptible pine forest type groups in the southeastern United States under climate change scenarios (total land surface area = 2 180 800 km^2).

	Precipitation change		
Temperature change	− 0.5 mm/day	Ambient	+0.5 mm/day
Ambient	533 600 (105)	507 625 (100)	485 150 (96)
+2 °C	645 675 (127)	622 275 (123)	599 550 (118)
+4 °C	774 025 (152)	749 500 (148)	722 900 (142)
+8 °C	972 650 (192)	958 225 (189)	943 175 (186)

Those projected area increases were apparent on the southern pine beetle outbreak scenario maps (Fig. 4). In contrast, the area occupied by south-eastern pine forests was projected to decrease slightly with increase in precipitation.

Outbreak ranges of southern pine beetle visibly extended northward with increases in temperature alone (cf. Figs 4a–d). In order to get an estimate of both northward and southward movements of the outbreak range under higher temperature, we superimposed the projected distribution at an increase of 8 °C on that at ambient temperature. We then summed the grid cells of the distribution at increased temperature that lay to the north and to the south of the distribution at ambient temperature and divided those totals by the number of grid cells across the east–west range of the distribution. This provided an estimate of the average number of 5 km × 5 km grid cells northward or southward at each east–west grid cell position that were

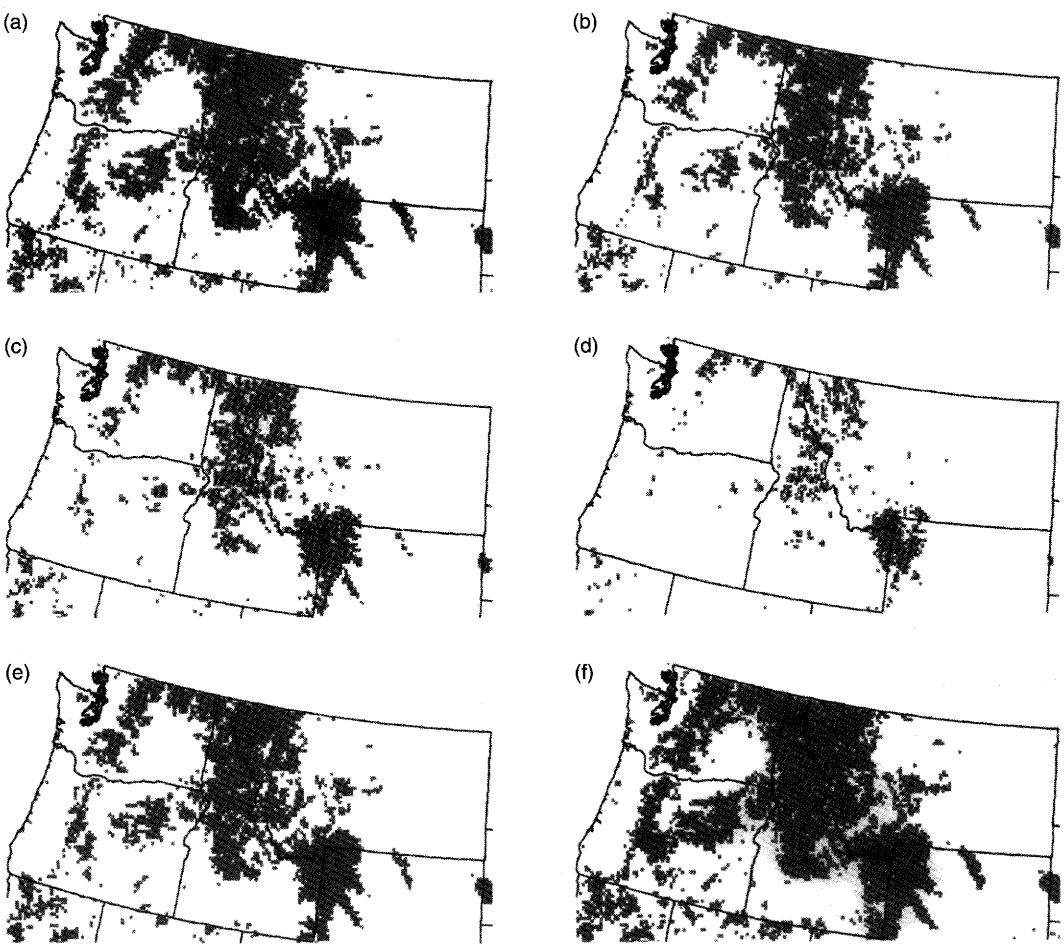

Figure 3 Projections of mountain pine beetle outbreak areas under changes in temperature and precipitation. (a) Ambient conditions, (b) warming of 2 °C, (c) warming of 4 °C, (d) warming of 8 °C, (e) ambient temperature and a decrease of 0.5 mm/day precipitation, (f) ambient temperature and an increase of 0.5 mm/day precipitation.

Table 8 Projected actual areas in km^2 and relative areas (in parenthesis, % of area projected at ambient conditions) infested by southern pine beetle under climate change scenarios (total land surface area = 2 180 800 km^2).

Temperature change	Precipitation change −0.5 mm/day	Ambient	+0.5 mm/day
Ambient	763 850 (90)	852 125 (100)	900 950 (106)
+2 °C	889 350 (104)	952 550 (112)	1 044 250 (123)
+4 °C	1 041 600 (122)	1 117 875 (131)	1 178 375 (138)
+8 °C	1 271 450 (149)	1 330 475 (156)	1 384 725 (163)

added due to the temperature change. With an increase of 8 °C, the northward shift averaged 159.8 km over an east–west range of 1500 km. A rather puzzling southward extension of the range was also evident in the maps. The southward shift averaged 91.9 km over most of the longitudinal range of southern pine beetle outbreaks. A similar analysis for the susceptible pine forests found an average northward shift of 183.4 km with an 8 °C temperature increase. Similar to the beetle outbreak distribution, the pine forest distribution also shifted southward at the highest warming scenario, extending an average of 42.9 km.

Discussion

Scenarios for the bark beetle species illustrated two of the range change patterns anticipated under global climate change (Porter *et al.*, 1991; Cammell & Knight, 1992). Mountain pine beetle ranges moved toward higher elevations, whereas southern pine beetle ranges generally expanded, with a net movement northward. Studies of range changes of insect species using their historical distributions, such as presented here, are relatively rare in the literature. One notable exception is the study of Parmesan *et al.* (1999), who analysed historical data on non-migratory European butterfly species to assess their range changes during the 20th century. Of 35 species, 63% exhibited a northward range shift by 35–240 km, whereas 3% exhibited a southward shift.

The ranges of host pine forests exhibited changes similar to those of the bark beetle species. Those forest changes provided much of the basis for changes in the bark beetle ranges, as reinforced by the discriminant analyses for beetle distributions, which consistently included forest type group occurrence as their first variables. Patterns of movement toward higher elevations and higher latitudes by tree species also have been predicted under global climate change (Davis & Zabinski, 1992; Franklin *et al.*, 1992; Iverson *et al.*, 1999).

Being strictly empirically based, our fitted model for southern pine beetle could not distinguish between the effects of host forest movement and temperature in setting the northern range limits of beetle populations. Our discriminant model for each bark beetle species consistently found the presence of infestation to be most highly correlated with the presence of a susceptible forest type, as is expected from knowledge of their ecology. Using a physiological approach, Ungerer *et al.* (1999) demonstrated that the northern limit of southern pine beetle is probably set by the lower lethal temperatures during overwintering. They suggested that southern pine beetle's host range is broad and that suitable host forests exist to the north of its current northern boundary. Thus, warming of the climate in North America could permit southern pine beetle survival north of the current range limit and open up new forest types to attack. Our climate change scenarios for southern pine beetle showed the same trends in range expansion as those of Ungerer *et al.* (1999). Although intrigued by their idea of climate change opening up new ranges of host, we are unable to test it with our model because the forest type group classifications available to us are rather general.

Using a modelling approach, Logan & Bentz (1999) demonstrated the potential for movement of mountain pine beetle populations to higher elevations and latitudes under a warming climate. In one case, they found warming by just 2.5 °C was sufficient to convert an unsuitable habitat to a suitable one, whereas in another they found warming by the same amount to convert a suitable habitat to one slightly less suitable but not prohibitive for mountain pine beetle. Although their model is not spatially explicit, its predictions suggest that mountain pine beetle may shift its range under climate change.

Our projections of northward movement of the northern boundary in southern pine forests averaged 183 km per 8 °C. In a similar vein, Iverson *et al.* (1999) projected changes in the optimal latitudes of several individual southern pine species under temperature change predictions for the Goddard Institute for Space Studies (GISS) (Hansen *et al.*, 1983) and Geophysical Fluids Dynamics Laboratory (GFDL) (Manabe & Wetherald, 1987) GCMs at doubled CO$_2$. For example, the optimal latitude of shortleaf pine, *Pinus echinata*, was projected to shift northward 180 km under the GISS predictions and 190 km under the GFDL. Similarly, the optimal latitude of loblolly pine, *Pinus taeda*, was projected to shift northward 40 and 130 km under the respective GCM scenarios. Overall increases in temperature in the south-eastern U.S. under the GISS model ranged from 3 to 8 °C, whereas those under the GFDL model ranged from 3 to 6 °C (Cooter *et al.*, 1993). Thus, our results for range shifts of southern pine forests are similar to those reported by Iverson *et al.* (1999), although they are not directly comparable because we focused on range changes of forest type groups rather than range changes of individual species.

Figure 4 Projections of southern pine beetle outbreaks in county areas under changes in temperature and precipitation. (a) Ambient conditions, (b) warming of 2 °C, (c) warming of 4 °C, (d) warming of 8 °C, (e) ambient temperature and a decrease of 0.5 mm/day precipitation, (f) ambient temperature and an increase of 0.5 mm/day precipitation.

Clearly such range changes for forests will occur over long periods of time under natural dispersal. For example, sedimentary pollen records from eastern North America and Europe suggest movement rates of 10–45 km per century as a result of warming following the last glacial period (Davis & Zabinski, 1992). However, with commercially valuable species, such as loblolly pine, rates of movement to higher latitudes are likely to be relatively high, as humans assist the process. Shifts in elevation, as predicted in the western pine forests, are expected to occur more rapidly than latitudinal shifts (Franklin *et al.*, 1992).

The effects of both human land use change and change in climatic variables other than temperature will complicate the forest range shifts further. The northward movement of southern pine forests in the south-eastern U.S. undoubtedly will not be as simple as indicated by our projections. Forest lands will compete increasingly with human land uses, including changing patterns of agricultural land use and the ever-increasing demands for urban and suburban development (Anon, 1989). Other aspects of climate change are also likely to affect future distributions of pine forests. For example, changing precipitation patterns will alter the frequency and geographical extent of fire and drought disturbances, complicating our ability to predict future forest distributions (Franklin *et al.*, 1992; Kurz *et al.*, 1995).

In contrast with the pine forests, the movement of bark beetle populations into new habitats made favourable by climate change will occur very rapidly because of their high mobility and rapid reproduction. Beetle populations should be able to track range shifts by their hosts easily. If climate change results in stress that is unfavourable to forest growth and survival (King, 1972; Kalkstein, 1976; Shrimpton, 1978; Gagne *et al.*, 1980), bark beetle activity may accelerate the disturbance at the lower latitudes and elevations, killing trees and hastening the northward and upward movement. In some areas, such as the eastern slopes of the Cascade Mountains in the north-western U.S., changing climatic conditions, perhaps coupled with increasing insect activity, may result in complete changes in vegetation type. For example, areas currently occupied by forests may convert to savanna and steppe (Franklin *et al.*, 1992). Another related bark beetle species, the spruce beetle *Dendroctonus rufipennis* Kirby, is currently undergoing outbreaks in south-central Alaska and causing such extensive damage to spruce stands that they are not regenerating rapidly and may convert to grasslands (Matthews *et al.*, 1997).

The different rates at which outbreak areas moved with temperature change relative to host forests suggest differing effects of climate change on the two bark beetle species. The rate of northward movement of southern pine beetle was similar to that of its host forests (i.e. 20.0 vs. 22.9 km/°C, respectively). In contrast, mountain pine beetle moved to higher elevations at nearly twice the rate of its host forests (30.2 vs. 15.5 m/°C, respectively). These results suggest that mountain pine beetle currently is limited more by temperature than is southern pine beetle.

Geographical range changes in response to increasing precipitation exhibited the same trend for the two bark beetle species and for the susceptible western forest types: areas increased as precipitation increased. This may reflect increasing areas of habitat favourable for tree reproduction and growth and hence bark beetle outbreaks, with additional moisture over the long-term. However, susceptible forest types in the south-east were predicted to decrease slightly in area with increases in precipitation. Results for the bark beetle species appear superficially to contradict the conventional wisdom that outbreaks are associated with periods of drought and tree water stress (King, 1972; Kalkstein, 1976; Shrimpton, 1978; Gagne *et al.*, 1980). However, the phenomena under consideration are at very different temporal scales. Outbreaks may continue to be influenced by water availability at the annual scale, but the long-term range changes of pine forests with increased precipitation ultimately may provide greater resource areas for bark beetle outbreaks on a time scale measured in centuries. It is interesting that the scenarios for southern pine beetle and the southern pine forests exhibited a southward shift along with the major shift to the north as temperature increased. We can offer no good explanation for this except to reiterate that the discriminant functions used are strictly fitted empirical models. As they model average behaviour, it is plausible that they will exhibit some tendency to 'balance' predictions, resulting in a less directional movement than we might anticipate. It must also be stressed that discriminant functions are linear models (Manly, 1986). It seems likely that some population responses to climate change will be nonlinear, and such nonlinearities may result in different projected trends of range change if incorporated in models. For example, the response of southern pine forests to temperature is likely to be nonlinear, and this may affect the movements of the northern and southern range boundaries. The southern boundary also may move northward, contrary to the prediction of our linear model. However, it is interesting that observations of actual range changes of bark beetles in Finland have not indicated simultaneous shifts of southern and northern margins of distributions in the same direction (Heliövaara *et al.*, 1991). That is, ranges do not tend to shift as blocks, but instead typically spread to the north while the southern margin remains fixed. Similar trends have been seen in predictions of the distributions of some pine species in the south-eastern U.S. (Iverson *et al.*, 1999).

In conclusion, our results demonstrate two patterns of geographical range shifts predicted in the climate change literature for two congeneric and ecologically similar bark beetle species. Relatively small changes in climate may shift the ranges of these species and the forests that they inhabit to higher latitudes and elevations over time. If they occur, such shifts may alter forested landscapes in the U.S. profoundly in the coming centuries.

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